

OBSERVATIONS ON THE OCCURRENCE AND HABITS OF THE *NACADUBA* COMPLEX OF THE LYCAENIDAE (LEPIDOPTERA), MAINLY FROM PUNE DISTRICT, WESTERN GHATS¹

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(With sixteen plates and seven text-figures)

The taxonomic work of Eliot (1973) stimulates the interest of the field naturalist. Distribution of the 71 species is tabulated and the possible origin and spreading of the group is suggested. Field observations on eight species from India and Sri Lanka are given, with notes on some early stages. The male genitalia and androconia are described and illustrated. Notes are added on the preparation of male genitalia.

CLASSIFICATION

For the purpose of this paper I include in 'Nacaduba and allied genera' those listed by Tite (1963), adding the single African genus *Pseudonacaduba* as in Eliot (1973) who divides the group as follows:

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|--|----------|
| a) <i>Petrelaea</i> section: | |
| <i>Pseudonacaduba</i> Stempffer, 1943. | African |
| <i>Petrelaea</i> Toxopeus 1929 | Oriental |
| b) <i>Nacaduba</i> section: | |
| <i>Nacaduba</i> Moore, 1881 | Oriental |
| <i>Prosotas</i> Druce, 1891 | " |
| <i>Paraduba</i> Bethune-Baker, 1906 | " |
| <i>Ionolyce</i> Toxopeus, 1929 | " |
| <i>Erysichton</i> Fruhstorfer, 1916 | " |
| <i>Catopyrops</i> Toxopeus, 1930 | " |

Eliot gives the following features generally common to the whole group: Veins 11 and 12 of the forewing are usually fused for at least part of their length. The eyes and the palpi are hairy. There are usually androconial scales on the upperside of the male forewings.

The two sections of Eliot, *Petrelaea* and *Nacaduba*, are sharply divided by clear differences in the genitalia (see Table 3).

In general appearance both sections are broadly similar, especially in the females. Males can often be distinguished by facies alone, but a close look with the lens is always necessary.

The position of the Nacaduba complex in the Lycaenidae:

The 'Nacadubas' belong to the subfamily Polyommatae Swainson, 1827, the so-called 'Weak Blues'; Eliot places them in the tribe Polyommataini Swainson. Since this unwieldy tribe does not fall into natural groups he divides them into thirty sections, mentioning where he considers them taxonomically close. The 'Nacadubas' fit into the tribe as follows:

The *Una* section is Oriental (Assam-Burma) and fairly close to the *Petrelaea* section. Next to *Petrelaea*, but not necessarily very close, comes the *Nacaduba* section, and this seems to be linked to the Oriental *Upolampes* section by the Papuan and Australian *Theclinesstes* section.

To the ordinary field naturalist, all this may seem a dry taxonomical bone. Yet two butterflies well known to him are now included in this *Upolampes* section; *Castalius caleta* and *Castalius ethion*, which should now be called *Caleta decidia* and *Discolampa ethion*. Thus

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OCCURRENCE AND HABITS OF THE NACADUBA

TABLE 1
DISTRIBUTION

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- A. *Pseudonacaduba* Stempfer, 1943.
African, two species, from Sudan southwards to Transvaal; Madagascar.
- B. *Petrelaea* Toxopeus, 1929.
Oriental, one species, ranging from India to the Solomons.
- C. *Nacaduba* Moore, 1881.
- (i) The Indian peninsula and Sri Lanka:
pactolus; extends through AB & Mal. to Torres Str., Phil. & Taiwan.
hermus; through AB to Mal. Phil. Moluccas.
olyetti; Sri Lanka only.
berenice; to AB, Mal., Phil., Moluccas, Aust., Solomons.
sinhala; Sri Lanka only.
kurava; to AB, Sul., Pap., C. York, Arnhemland, Solomons, Japan.
beroe; Sri Lanka. (apparently *not* peninsular India) AB, Mal., Phil., Taiwan.
calauria; Sri Lanka (*not* India) Mal., Moluccas.
 - (ii) Assam, Burma, Malaysia, Papua, Australia, Melanesia, Polynesia:
Twenty-nine species.
- D. *Prosotas* Druce, 1891.
- (i) The Indian peninsula and Sri Lanka:
nora; Assam, Burma, Malaysia, Philippines, Cape York, Taiwan.
dubiosa; Assam. Burma, Malaysia, Papua, Queensland, Solomons.
noreia; Assam, Burma to Malaysia.
 - (ii) Kumaon, Assam, Burma, Malaysia, Papua, Australia, Taiwan:
Fifteen species.
- E. *Paraduba* Bethune-Baker, 1906:
Three species, Papuan.
- F. *Ionolyce* Toxopeus, 1929.
- (i) The Indian peninsula and Sri Lanka:
helicon; to Assam, Burma, Andamans, Nicobars, Malaysia, Queensland. Torres Strait.
 - (ii) *brunnescens* Tite, 1963. Solomons.
- G. *Erysichton* Fruhstorfer, 1916.
Three species: Moluccas, Papua, Queensland.
- H. *Catopyrops* Toxopeus, 1930.
Five species: Burma, Malaysia, Papua, Solomons, Queensland, New South Wales.
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Notes to Table 1.

This Table attempts to give a general picture of the distribution, showing that the greater number of the sixty-nine species is found in SE Asia. Many of the widely distributed species have formed subspecies.

Abbreviations:

- AB — Assam-Burma.
Mal. — Malaysia.
Phil. — Philippines.
Sul. — Sulawesi (formerly Celebes).

these familiar jungle insects turn out to be quite near the 'Nacadubas' and a long way from their former neighbours like *Castalius rosimon* and *Tarucus*, typically plains insects. This is just one example of how the attitudes of the field naturalist and of the laboratory worker support and complement one another.

ZOOGEOGRAPHY

When one has been privileged to encounter a few members of an intensely interesting group in the field, questions about their origin and evolution press for an answer. In the nature of things, absolute certainty is unattainable, but it would be a poor response to the complex beauty of these little creatures if one shirked the risk of a few guesses.

So I imagine myself back on a rather denuded part of the Western Ghats. There is *nora* — (or *dubiosa*; I hope, *noreia*) — dashing around an acacia bush in the midday heat along with three kinds of *Azanus* and a *Rapala*. How did these forms get here? During what unimaginable time have they been going through a cycle of courtship, egg-laying and growth, in dependence on a plant like this, with ants like these busily walking about its twigs and blossoms?

Now I move on into deeper forest, into remains of climax jungle ... how long has *pactolus* been living on and on in this tiny area where I stumbled upon it twenty years ago? Those great *Entada* limbs must have been seedlings in Shivaji's day; but the lianas of those times would only take you back another three hundred years. We have to peer back far beyond this ... It is time to look calmly at the question of the origin and evolution of the butterflies, and to see if there can be any justifiable guesses about the 'Nacadubas'.

There is only the scantiest fossil record for

the butterflies, from the early Tertiary, around fifty million years ago. A few actual butterflies have survived in the Baltic amber, from the mid-Tertiary; these and the fossils are referable to existing families. But recently a probable Lepidopteron from the Triassic, around 200 million years ago, was described from a fossil. So far, this fossil from Australia is the only actual evidence of the development lying behind our present Lepidoptera. [Authority quoted by Higgins (1975): 31].

The picture can, however, be filled in to some extent through recent work on the early history of the planet, especially the now well established phenomenon of Continental Drift. [See Eliot (1973): 457-465]. In what follows, I am greatly indebted to Col. Eliot's paper; any mistakes and misinterpretations are my own.

Eliot (op. cit.): 460, giving his authorities, places the origin of the butterflies, as a Sub-order, in the late Mesozoic era around the middle of the Cretaceous period, about a hundred million years ago. (For a time scale, see Table 2 throughout). The most likely area for the emergence of the group would be the enormous southern continent of Gondwanaland; it was mostly tropical; later enormous forces would break it up into the present lands we know as Africa and Madagascar, India and Sri Lanka, South America, Australasia and Antarctica. (Plate II).

During the Cretaceous the climate was warm, the lands flat and close together, the seas at their maximum. Generations of tiny molluscs were depositing their shells on the sea beds, laying down the chalk. On land, the giant Dinosaurs were nearing their rather sudden extinction. Flowering plants were evolving in symbiosis with the new nectar-sucking bees and Lepidoptera.

Such was the world of the first butterflies. Among them would be the *Lycenoidea*, from

which would develop — when, we cannot tell — the two groups Riodinidae and Lycaenidae. From the vast, tropical spaces of Gondwanaland it would have been easy for butterflies to colonize the northern landmass of Laurasia where the climate would be at least partly subtropical. Laurasia included what are now North America, Greenland and Eurasia, and was attached to the northwest of Gondwanaland where Spain now faces Africa, and at various points west.

Thus one can accept that in the mid-Cretaceous there were no ocean barriers prohibiting the colonisation by butterflies of all suitable land. The fossil record bears this out; at this very time the marsupials spread worldwide.

Before the end of the Cretaceous, a major rearrangement of the land-masses began, due — it is now widely held — to the action of Continental Drift. The process still continues today, at rates varying from 12 to 150 millimetres a year. The rock plates of which the earth's crust consists tend to push over one another, riding upon the viscous mantle which supports them. In this way the land surfaces which appear so stable to the senses are, in fact, on the move, and get carried long distances in the course of a few million years.

By about 90 million years ago the south American part of Gondwanaland had drifted westward; Antarctica, with Australasia, southward; India, perhaps with eastern China, north-eastward across the immense Tethys Sea. Thus the African heart of disintegrating Gondwanaland would still contain the majority of Lycaenid forms. Since India had become isolated in the ocean, probably long before the mid-Cretaceous, it is unlikely to have had 'a Lycaenid fauna until its northward drift brought it close to, or even in contact with, Eurasia'. [See Eliot (1973): 461]. The same would apply to Australasia; Australasia and India

would have had rather cold climates until they came near or fused with Eurasia. On the other hand, Eurasia in Cretaceous and Paleocene times was further into the tropics than it is today, and was in close contact with Africa through the Gibraltar link. Thus in the early Tertiary many Lycaenids could have reached even southeast Asia — at a time when India had not yet arrived at its present location.

By about 65 million years ago, during the Tertiary, Eurasia began to get colder as the result of a northward drift. Also the Sahara desert was appearing. This meant that tropical Africa, with its Lycaenids, became isolated on all sides. Especially in the rainforests, ancestral populations continued to develop for the next 60 million years or so.

Then, at the end of the Tertiary, the Himalayan upsurge began. This was the most momentous of all earth changes for present life forms. Enormous bucklings and foldings of the rock pushed up chains of new mountains from what had been a comparatively flat world. Their still jagged and unworn ridges, so unlike the ancient profile of the Ghats, include the highest points on this planet, and sweep in a great curve from Papua to the Alps.

For the Lycaenidae this meant they ceased to be isolated, and would soon have new lands before them. Drift and other earth movements fused India with Eurasia and formed a middle eastern link with northeast Africa. The Tethys ocean therefore was no longer a barrier; land near its northern shores would now become a bridge. (See Table 2).

The juncture of India may not have been completed until ten million years ago, and another five million may have passed before the Australasian group arrived near its present position. But as soon as the ancient Indian island had settled as a peninsula south of the new Himalayas, something like the present

climatic rhythm would have begun. Many Lycaenidae would now have been able to enter India from Africa through the northeast link, and in the course of time adapt to new conditions — from plains to hills, from rain forest to monsoon forest. Their infiltration would not have been difficult, since the middle East was not yet largely desert, nor broken up by the Red Sea and the Persian Gulf. Even now there may be some transfer of Lycaenids by this route still going on. See Eliot (op. cit.): 461. For instance, two Thecline genera which can put up with at least semi-desert conditions are *Aphnaeus* and *Spindasis*; among Polyommatae, *Azanus*, and, I would suggest, *Zizeeria* and *Freyeria*, are about as desert-tolerant as small butterflies can be; *A. jesous* is found all the way from north Africa to Burma. The present distribution of species in the *Spindasis* group is notably in favour of transfers from Africa eastwards. We should not have in mind a picture of migration, but rather of questing and testing, over immense periods, and literally from bush to bush.

But in Eliot's opinion the 'Nacadubas' did not reach India by the north African route. Compared with the *Theclinae* they are weak flying and of delicate structure, yet they have reached Queensland in some cases and even New South Wales. New Guinea and Melanesia are full of them; a glance at Table 1 shows their heartland is southeast Asia. In contrast, really tough creatures like *Spindasis* have not crossed Weber's Line. See Plate I and Eliot (op. cit.): 462; their present distribution adds weight to the belief that they belong to the north African movement. Along with other Lycaenid groups they reached southeast Asia through India in 'post-Miocene times and ... underwent secondary development in India ... and the Sino-Himalayan subregion.' (Eliot, loc. cit.). There are about fifty *Aphnaeus*-*Spindasis* species in the Ethiopian Region, and

only fourteen in the Oriental. But the latter differ little from their African relations, so, as Eliot says, long isolation is out of the question.

In contrast, there are over sixty species of the *Nacaduba* complex in the Oriental Region, of which only a dozen occur in India and Sri Lanka, and a mere two in the Ethiopian Region. Eliot believes that the ancestors of *Nacaduba* and some other Polyommatae groups reached tropical Asia from Gondwanaland right back in the Cretaceous. They developed there until the Pliocene, a moderate number of forms reaching India after its fusion with Asia.

Eliot refers to the belief of Zeuner and others that there was a Protopapua, covered with rainforest, north of the present site of New Guinea and connected with the Asian mainland by strings of islands. Protopapua is thought to have lasted from the early Tertiary until the mid-Miocene, when the mountains of New Guinea began to appear as a result of the great upsurge. Both lands may have co-existed for a time, allowing butterfly populations to transfer. See Eliot (op. cit.): 463, and passim. Even without a Protopapua there must have been vast areas in Asia where 'Nacadubas' could have proliferated and formed species, especially in conditions of isolation. And there was plenty of time for it, probably some forty million years.³

Eliot, therefore, has not simply made deductions from present distribution; he has given us a brilliant reconstruction of the butterfly past, using the few but significant probabilities of prehistory in conjunction with the meagre fossil record.

The 'Nacadubas', being rather sessile creatures, have a tendency to form races, and these

³ It is usually held that a species may evolve in from half a million to one million years, and a subspecies in about ten thousand years.

are likely to be incipient species. This tendency has been encouraged by changes in sea level during geologically recent times. From about 240,000 years before the present, until about 180,000 years BP, there occurred the last of the Pleistocene glaciations in the northern hemisphere.⁴ The ice held up so much seawater that the Sunda and Sahul Shelves in the shallow Indonesian and Australian seas were exposed. (See Plate I). The new land developed rainforest, the Sunda forest being about a million square miles in extent. When the ice receded, releasing the seawater, numerous islands remained and are still there, with the remnants of their rainforest. As long as man does not ruin them, these relict environments will continue to foster speciation. Thus there are five or six races of *Nacaduba astarte* on closely adjacent islands or groups of islands in the Solomons and Bismarcks. See Tite (1963): 76, and Plate III.

Even if new evidence should modify Eliot's conclusions, his main theme will stand, based on the near certainty that during the Mesozoic the continents were also together if not completely united. The existence of Gondwanaland during this era seems proved by the distribution of *Lystrosaurus*, a small freshwater reptile, in the Triassic beds of both Africa and India. Recently it has been discovered in the Antarctic. Another reptile, *Mesosaurus*, from the Permian, links southern Africa and Brazil. A Permian plant, *Glossopteris*, has long been known from all the components of Gondwanaland. The parts of Laurasia are linked by equally impressive evidence from fossil reptiles and amphibians. See Colbert (1973):

On this basis, therefore, it is clear that the Butterflies, including the remote ancestors of *Nacaduba*, could have been flourishing in the

former great Gondwanian continent towards the end of the Mesozoic. They could have reached southern Asia as early as the Cretaceous, when all the lands were still close together, and continued to evolve over these very lengthy periods. They Polyommata genera, perhaps with *Nacaduba* among them, spread first to the Papuan subregion, and later, during the major earth changes of the Tertiary, arrived in India.

Note on the Photographs of Adults.

The specimens used for *Nacaduba beroe* (male) and *N. sinhala* (male) on Plates VII and X have lost the filamentous 'tails' at v. 2 of the hindwing.

Apart from these the Plates depict species actually either tailed or tailless.

Notes on some species from India and Sri Lanka

1. *Petrelaea dana* (DeNiceville, 1883) (Plates V & VI)

This is a wide ranging species, from India to the Solomons, but it has not been possible to define any geographic races [Tite (1963): 109]. It is uncommon in the places I have visited, and I saw it on only two occasions. The first was, surprisingly, in a crowded part of Bombay city when I took a male fluttering over garden beds in St Peter's School compound, which lies immediately below a small eminence known as Mazagaon Hill. At that time (January, 1953) there was a good deal of rough ground there apart from the public gardens, also a water tank and many trees, so the hill was attractive to butterflies. Although only a few metres high, it constitutes a land mark for insects crossing Bombay harbour or working in through the suburbs from the Salsette jungles. I believe a good deal of migration in the full sense, and also drifting, takes place from Salsette out to Malabar Hill; I have caught or observed several butterfly species,

⁴ Not the more localized glaciation, often called 'the Ice Age', of 120,000 to 22,000 years BP.

TABLE 2
TIME SCALE, BASED ON COLBERT (1973): 24

Era: Length in millions of years	Periods and Epochs	Duration in millions of years	Duration, before the present	Events and Life forms
Cenozoic 65	<i>Quaternary:</i>			
	Pleistocene	3	20,000-3 mill.	Man.
	Pliocene	9	3-12	Australia near present position.
	Miocene	15	12-27	Juncture of India. New Guinea replacing Protopapua.
	<i>Tertiary:</i>			
	Oligocene	10	27-37	Modern mammals. Himalayan upsurge beginning.
FOSSILS OF LEPIDOPTERA.				
	Eocene	18	37-55	Flowering plants dominant.
	Paleocene	10	55-65	Primitive mammals. ? Protopapua.
Mesozoic 160	<i>Cretaceous</i>	70	65-135	Ancestral mammals. Flowering plants begin.
	<i>Jurassic</i>	60	135-195	Giant Dinosaurs. First birds. Dragonflies Grass- hoppers Sawflies. ? Ants.
	<i>Triassic</i>	30	195-225	First Dinosaurs. Conifers, Cycads, Small Ferns, Gingkos.
Fossil of a(?) Lepidopteron from Australia.				
Paleozoic 375	<i>Permian</i>	55	225-280	Early Reptiles.
	<i>Carboniferous</i>	65	280-345	Large Amphibians, Early Plants, Beetles, Bugs, Cicadas.
	<i>Devonian</i>	50	345-395	First Insects — <i>Aptera</i> .
	<i>Silurian</i>	45	395-440	First backboned animals.
	<i>Ordovician</i>	60	440-500	
	<i>Cambrian</i>	100	500-600	
Precambrian time about 3½ billion years.				

including Lycaenids, which can hardly be resident in the city or are not proved to be so. This has been noticed by Sanders (1955). It is on the other hand possible that there are small relict populations from former jungle or in surviving jungle within the city limits. One such place which I was able to visit on rare occasions is Governor's Beach on Malabar Hill, where I saw the magnificent Great Orange Tip *Hebomoia* for the first time. It would be good to seek permission to investigate this area. As for *Petrelaea*, until there is further information it should be regarded as a stray in the city, and searched for in Salsette localities like Vihar and Powai.

My second encounter with *Petrelaea* was on Katraj Ghat near Pune at c. 850 m., where I took a male at a damp patch in October, 1961. I would say this was a typical habitat. Bell (1918): 653 implies that it is rare or local on the Western Ghats. He says it is especially fond of *fresh* cattle droppings, so these should be watched. (Many Lycaenids will never be noticed at all until one hits upon the exact places which attract them, or which the great naturalists, like Bell, have already discovered).

The species may be commoner farther south on the western Ghats. My friend Mr. A. J. Sharman found it abundant at about 1370 m. in the Biligirirangan Hills. Karnataka, in May 1957 along forest streams; at Kallar in the Nilgiris at c. 370 m, in April; localities in the Palnis at c. 2134 m. in May and August; and a place in the Tirupati Hills (Eastern Ghats) at about 400 m. in June. All his specimens were males taken at mud; he saw no females anywhere. Dr T. Norman, who most kindly gave me a male from Assam and a female from Manipur, said that the female is rare in the Assam Valley plains. Woodhouse & Henry (1942): 91 state that the species is never

common but occurs all over Sri Lanka below c. 460 m. all the year round. The males come to damp spots; the females are very rare.

Unless rearing from the early stages should prove otherwise, I think it preferable to say that the female of *Petrelaea* is rarely taken; it probably has skulking habits and lays its eggs on plants growing in out-of-the-way places, which would explain why the early stages have not been observed. The sexes appeared in about equal proportions in the two *Nacaduba* and the two *Prosotas* species of which I have some rearing experience.

It is interesting that the upperside blue of the male is fairly bright and clear, similar to that of the African *Pseudonacaduba sichela*. How closely *Petrelaea* and *Pseudonacaduba* may be related is a matter for argument; their genitalia are different except for one striking similarity. See Eliot (1973): 379, where he says it is unwise to give absolute primacy to any one character.

The Androconia

These are specialized scales found in patches or scattered on the wings of male butterflies of several families, including the Lycaenidae. Their occurrence in any Lycaenid genus seems random. Their physical structure, when seen with the scanning electron microscope, has often been found to differ from the ocular view; see Eliot (1973): 399. They are taken to be scent scales.

In *Petrelaea* the androconia are club-like and remarkably long for a small butterfly [see Plate IV: 4 and 4(a), the latter figure drawn at a lower magnification in order to include the whole.] Such scales are found in a few other species: *Erysichton lineata* (Murray) of the *Nacaduba* complex, where they are quite twice as large as in *Nacaduba*; see Tite (1963): 102. A *Jamides* species; see Eliot (1973): 406. *Azanus ubaldus* Cr. where they are about the

same length as in *Petrelaea*. The occurrence of scales of this type seems random, although one could say that the first three are not too widely separated in classification. *Azanus* is shown on Plate IV: 5 at the lower magnification.

The androconia of *Petrelaea* appear to have eight or ten longitudinal ridges, judging from the four spaces usually visible between the ridges. Scattered along these ridges, mainly at the broader end, appear to be nodules or pits. In view of what is said above about the physical structure, all statements here are provisional. The drawings show what is seen with the ordinary microscope; except for the two cases noted above they are all at the same magnification, done with a *camera lucida* arrangement devised by Mr. Tite.

The precise use of the androconia has not been observed in the Lycaenidae so far as I know; almost certainly they are scent producing scales used in courtship. Tinbergen (1974): 138-157 describes the arduous investigations needed to discover the role of scent in the courtship of a Satyrid butterfly in Holland. No less perseverance will be needed if anyone with the opportunity is to do similar work with Lycaenidae.

The Male Genitalia

I include here some general remarks applying to all the genitalia studied here. Particular statements apply only to *Petrelaea*. *The Aedeagus* (a word perhaps connected with Latin *aedes*, meaning a house) is the hard outer casing or housing of the penis. In this small species it is c. 1.75 mm long, as compared with c. 0.9 mm in the large species *Nacaduba pactolus*. The *ductus*, the duct leading from the seminal vesicles, enters the aedeagus ventrally in *Petrelaea*, dorsally in the *Nacaduba* group. In Plate X: 6 the ductus is shown by broken lines on the left, near the base of

the aedeagus, the pointed organ which reaches diagonally across the figure. Since the ductus is of soft tissue, or only lightly reinforced, I have not been able to retain it in any of my dissections. (The genital organs are made of the same sort of hard material, known as chitin, which support the insect body, so that only the soft parts, muscles and ligatures, are lost when making a microscope slide). The aedeagus in *Petrelaea* has no Chapman's process; this is a feature of many species of the *Nacaduba* section, arising ventrally from the upper part of the aedeagus. In *Petrelaea* there is a dorsally placed organ, shown in side view in the figure. A dorsal view shows that this feature grows from the surface of the aedeagus about halfway up, and ends about 2/3 of the way along towards the tip. This process ends in the shape of a two-pronged fork sloping a little away from the surface of the aedeagus (See Fig. 1).

The Uncus (Latin = hook or barb) is attached to the dorsal side of the genital ring. In most Lycaenid genera the uncus is divided into two lobes (labides), each of which bears a curved brachium (Latin = arm). The latter are better referred to as *falces* (Latin *falx* = sickle) which describes their usual shape.

In Plate X: 6 only the right labis is shown. There does not seem to be anything special about these structures in *Petrelaea*.

The Valvae (valves, clasps or claspers) are attached to the ventral side of the genital ring. Higgins (1975): 95 says they are not well named as clasping organs since they are relatively immobile. At the base of the valvae is the furca or fork, known also as juxta or join. Its function is to help support the aedeagus. In Plate X: 6, the furca is shown in position; it is not clearly seen by transparency in the slide. Plate X: 7 shows the inside of the right valve; in *Petrelaea* the hook at the valve tip is directed ventrally. In Plate X: 6

the nearer valve is rather edge-on, but the other valve shows the true direction of the hooked tip.

The Vinculum (Latin = bond or fetter) is the genital ring, actually U-shaped, to which the labides are attached dorsally and the valvae ventrally [See Higgins (1975): 27, 95-96].

Burma westward, but is not rare in the Khasis [See Cantlie (1952): 52]. Dr T. Norman told me that it was quite common in the 1960's in the Khasi Hills, flying up to c. 1200 m. H. C. Tytler (*JBNHS* 21: 595) reported it up to 1500 m. in the Nagas. Bell found it in the Karwar jungles in the 1920's, and probably reared it, since there are pupa skins under two of his specimens in the collection

TABLE 3

COMPARISON OF THE MALE GENITALIA IN THE *Petrelaea* AND *Nacaduba* SECTIONS.

<i>Petrelaea</i> section	<i>Nacaduba</i> section
Aedeagus:	Aedeagus:
a) Long.	a) Short.
b) Ductus enters ventrally.	b) Ductus enters dorsally.
c) Subzonal and suprazonal portions about equal.	c) Suprazonal portion shorter.
d) No coecum.	d) A short coecum usually present.
Vinculum:	Vinculum:
. Saccus developed.	Saccus not developed.

Notes to the above:

The Zone (Greek = 'girdle') is the point at which the penis is fixed to the inside of the aedeagus. Its position can usually be seen, but is hard to depict in a line drawing.

The Coecum (Latin = 'blind') refers to the basal part of the aedeagus.

In *Petrelaea* the process from the vinculum known as the *saccus* is well developed, extending forward into the abdominal cavity, evidently in order further to stabilize the genital armature. The word *saccus*, meaning 'bag', is therefore not apt, although it is the name in use. A long *saccus* seems (understandably) to go with a long aedeagus [Higgins (1975): 28].

II. *Nacaduba pactolus continentalis*

Fruhstorfer, 1916.

(Plates VI & VII)

This fine species ranges in a number of forms from the Western Ghats to the Torres Straits, and from Sulawesi to Taiwan, trenching both on the Palaearctic region and on the Australian part of the Oriental region. The race *continentalis* occurs rather rarely from

of the Bombay Natural History Society; no other information was found.

I had the good fortune to be able to rear it from a colony discovered in the neighbourhood of Khandalla, 500-700 m., Western Ghats, as recorded in Bean (1965): 614-626. The following assesses the information obtained:

Bell's material, cited above, shows that in Karwar the butterfly appears in the hot season (March-May); Tytler, as above, reported it for July; material in the collections of the British Museum (Nat. Hist.), of the Bombay Natural History Society, and of the Hope Collections, Oxford, also bears hot-season dates and, in some cases, of the post-monsoon period. But these times of appearance differ in the Khandalla region; I never

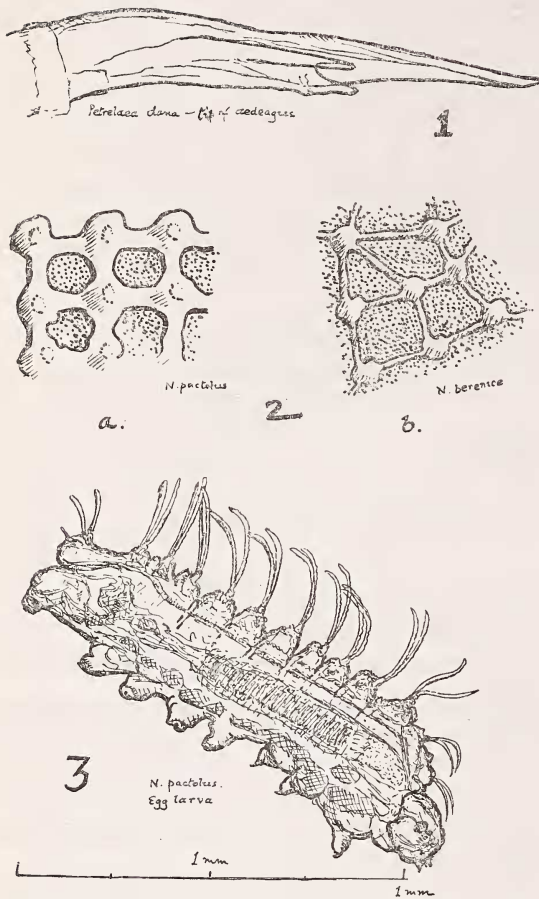


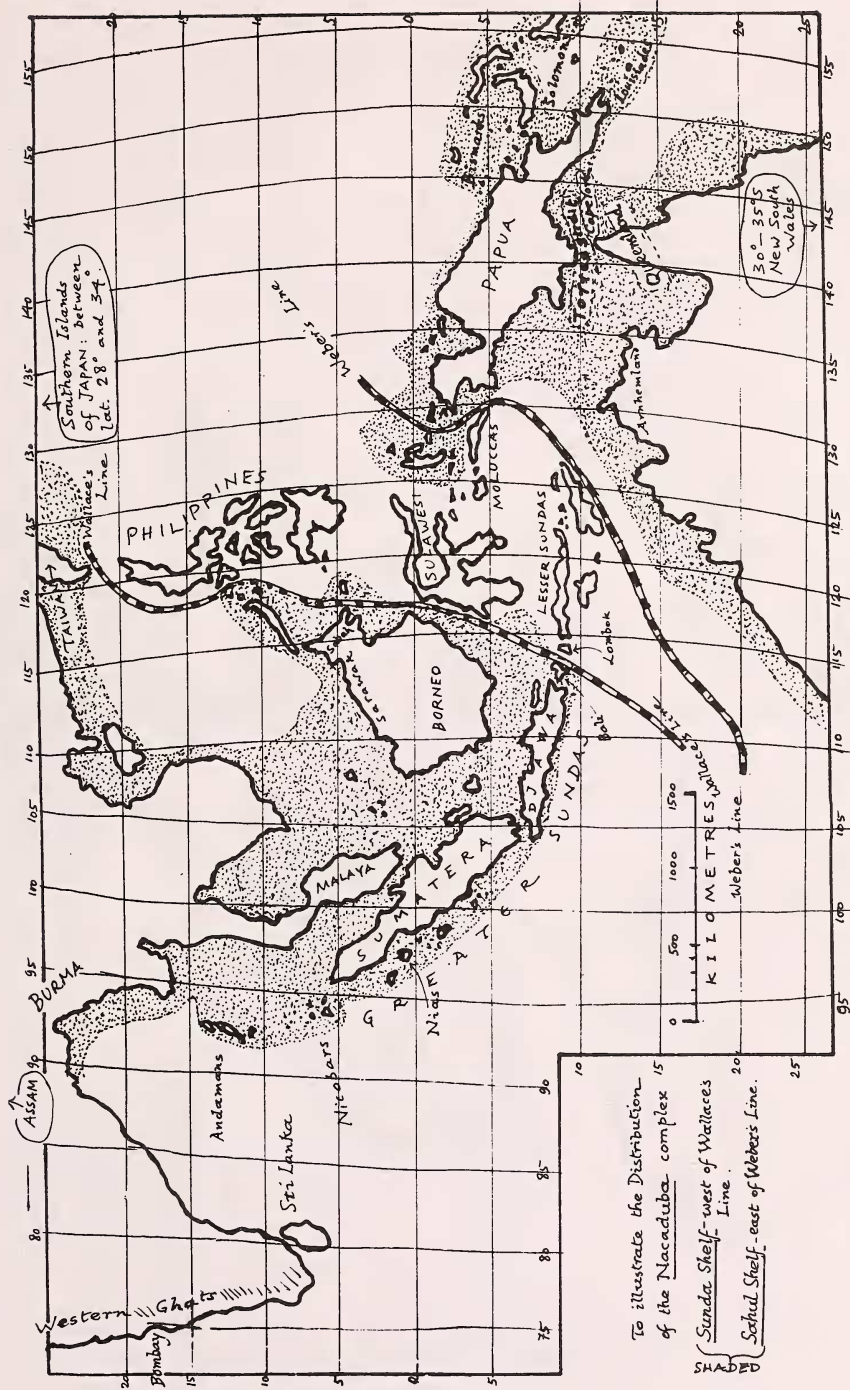
Fig. 1. Tip of the Aedeagus, *Petrelaea dana* (Diagrammatic). Fig. 2. Sculpture on the egg: a) *Nacaduba pactolus*; b. *N. berenice*. Fig. 3. Egg-larva: *Nacaduba pactolus* — W. Ghats, Sept., 1964.

saw the insect there between December and July. Between 1956 and 1964 I was able to make careful observations at intervals of two or three weeks, which indicated that *N. pactolus* is an entirely monsoon and post-monsoon insect in its Khandalla locality. It would seem that conditions are not damp enough there for it to develop adults in winter and spring as, for instance, *N. berenice* is able to do. The *pactolus* larvae need the tenderest leaves of the food plant, preferably the youngest red ones, which are photosynthesizing

at a great rate and are full of carbon. Upon such leaves the larvae can develop rapidly. Except in the wettest jungles, as in Karwar and Assam, rapid growth is probably essential. Bean (1965): 620, observed that the period from egg to adult may be as short as 25 days; thus between July 21 and November 23 (the observed flight period) as many as six generations could be born while enough food was still in a condition favourable to growth.

In Khandalla the only foodplant observed was *Entada pursaetha* D.C., an impressively large creeper which at full growth reaches with massive contorted limbs right up into the forest canopy. The larva will not eat *Mezoneurum*, which is much commoner in the habitat than *Entada*, and also a leguminous species. A laying female was seen not to be interested in *Mezoneurum*; the individual mentioned in Bean (1959): 650-651 seems to have been trying to differentiate between these two plants which were tangled together.

It would be of great interest if someone could visit the Karwar jungles for this species, and try and find out what it lays on there, and check the extent of the flight period. At Khandalla there is a diapause from the end of November until July, but this may not occur in wetter places, or may be shorter. Khandalla is probably the westernmost edge of its range, where it seems to have adapted to drier conditions. One assumes that it is as a pupa that it lies over from late autumn until the monsoon is well established, but this has to be proved. It could be done if one had facilities for caging or sleeving larvae on growing *Entada* towards the end of the flight season. It would have to be in the jungle or near it, so that conditions as close to nature as possible were provided; and the worker would have to be ready for many disappointments and setbacks, including those from the destructiveness, curiosity or ignorance of human beings.



The Distribution of the *Nacaduba* complex.

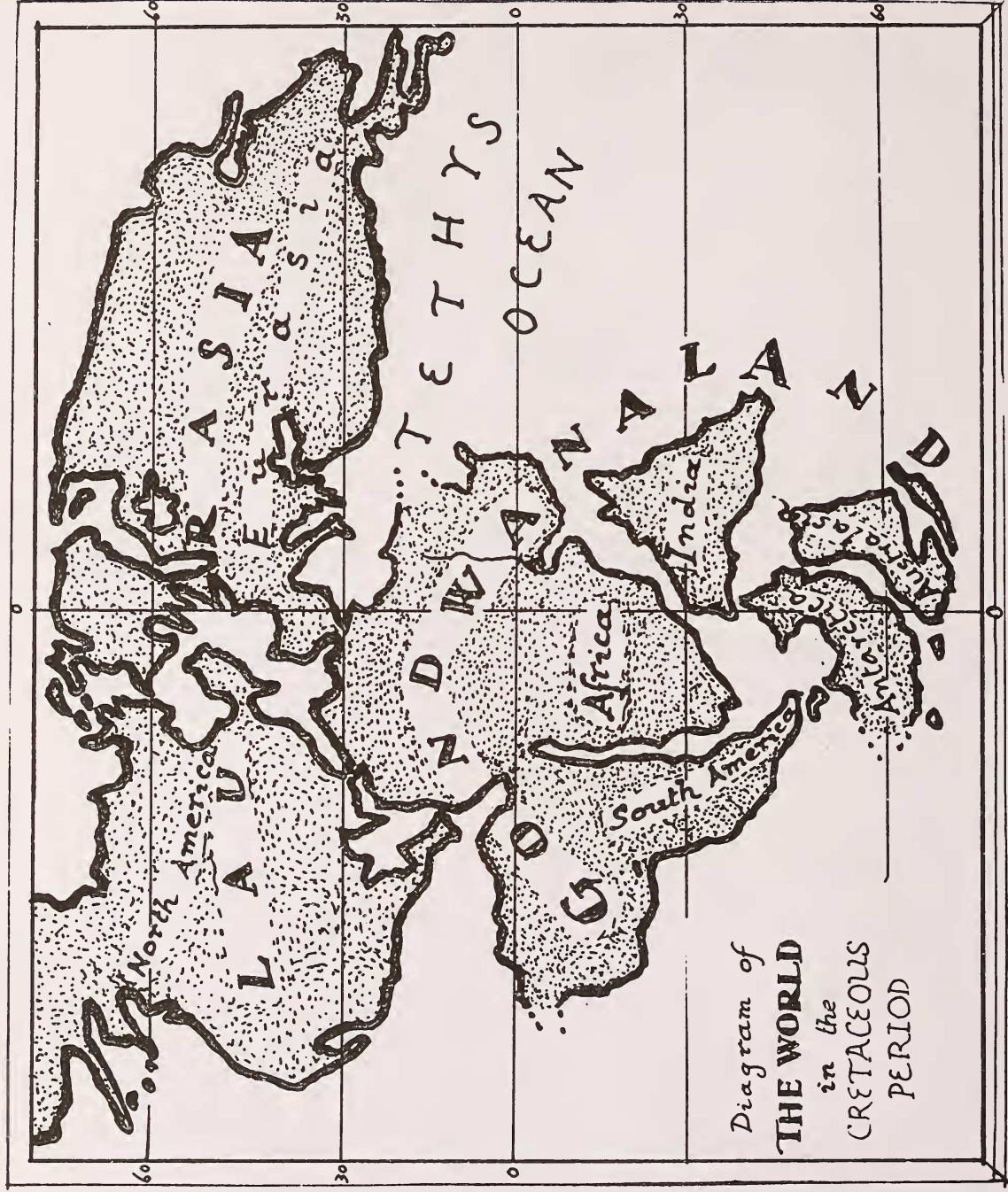
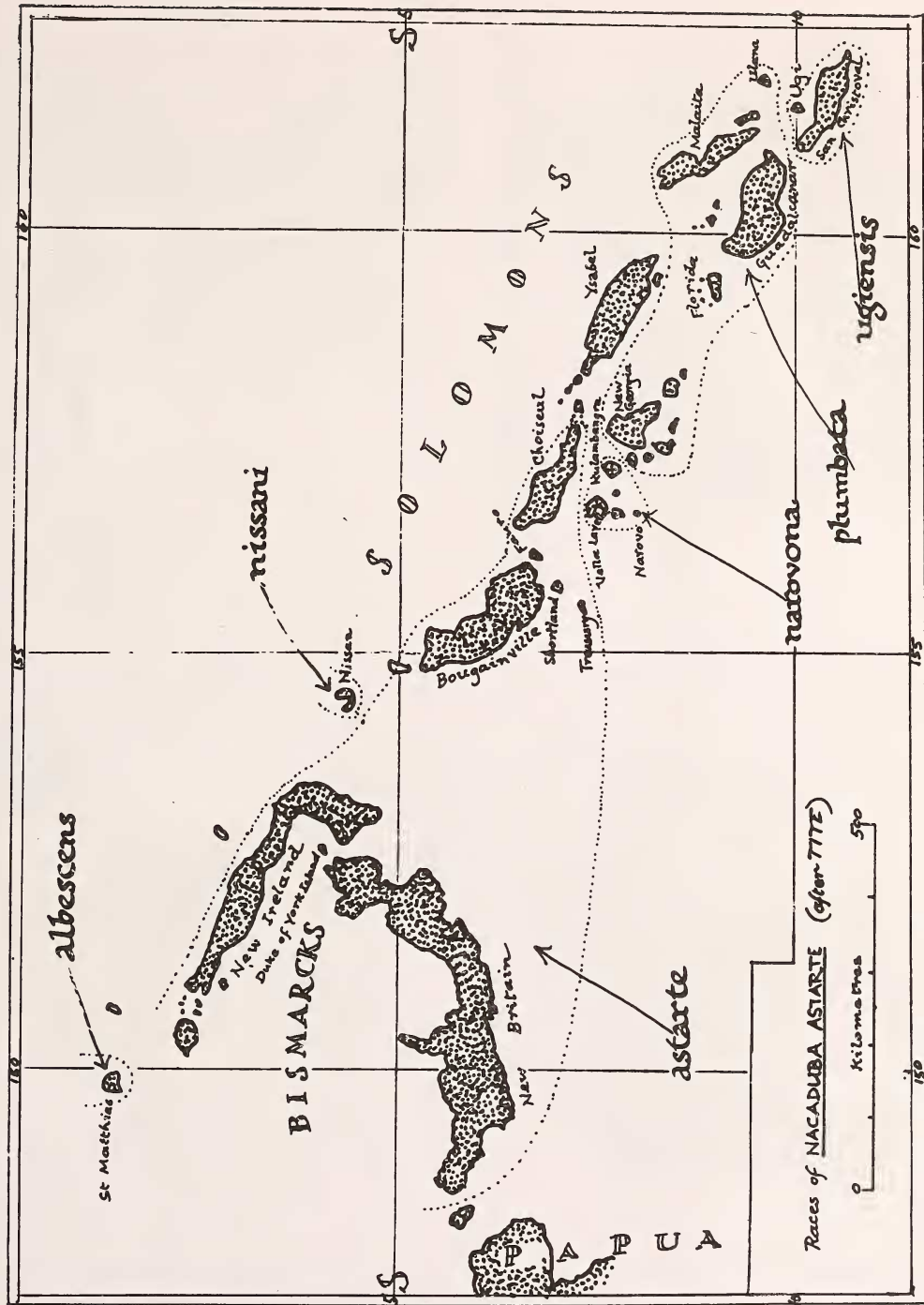
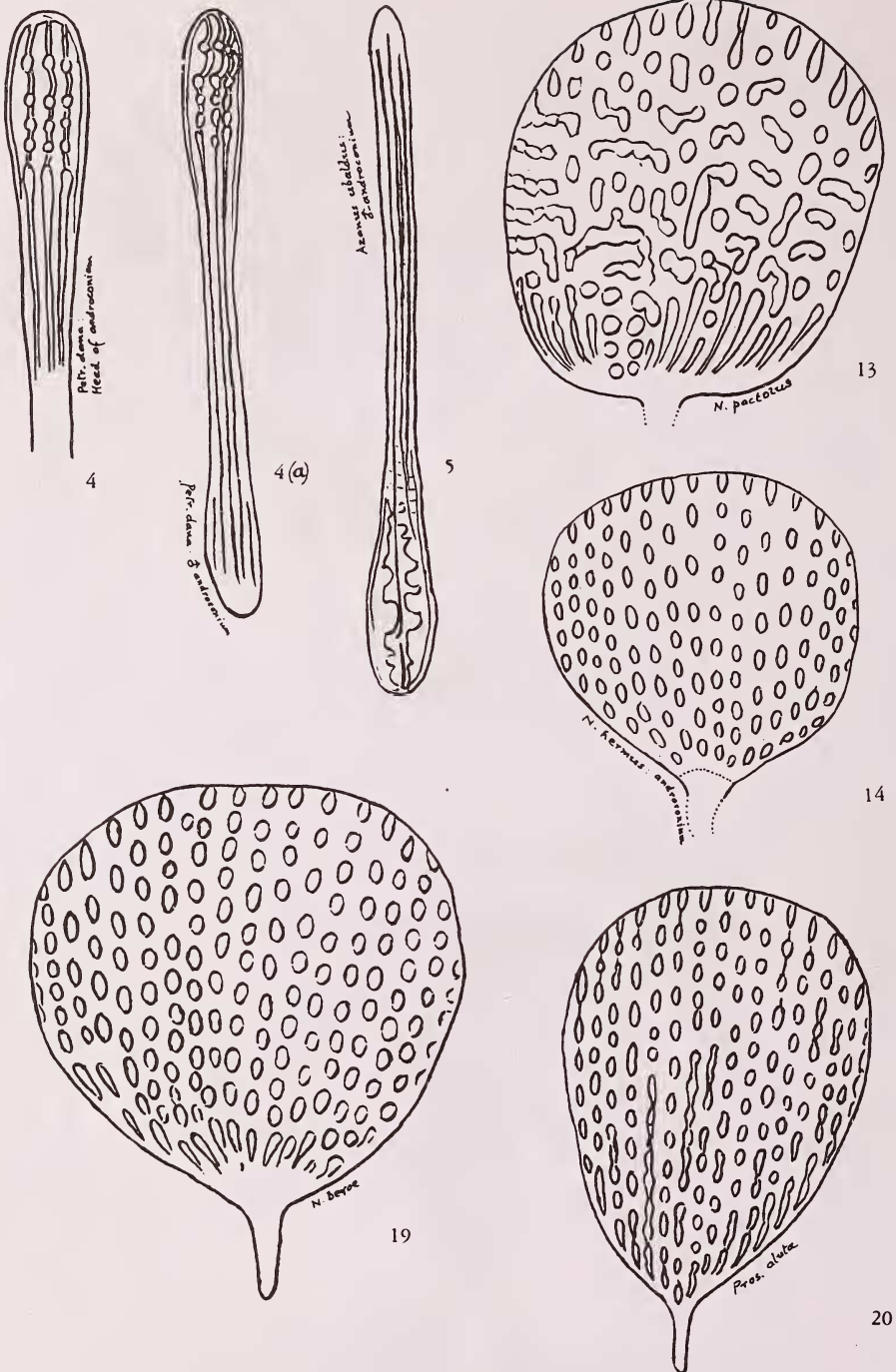


Diagram of the world in the cretaceous period. (Around 70 million years BP).

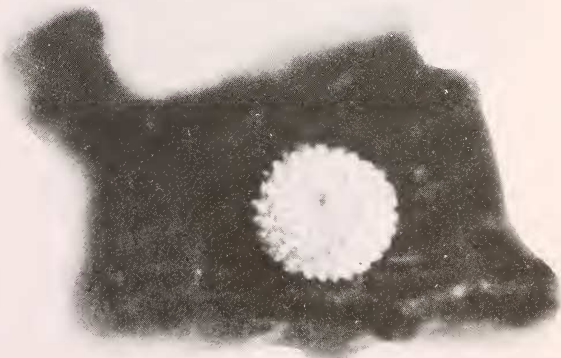
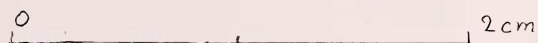
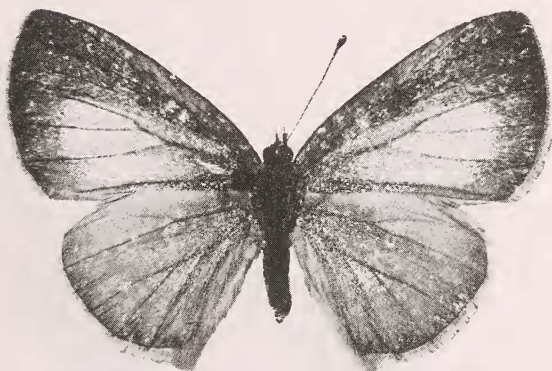
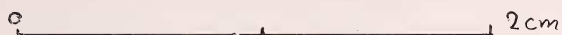
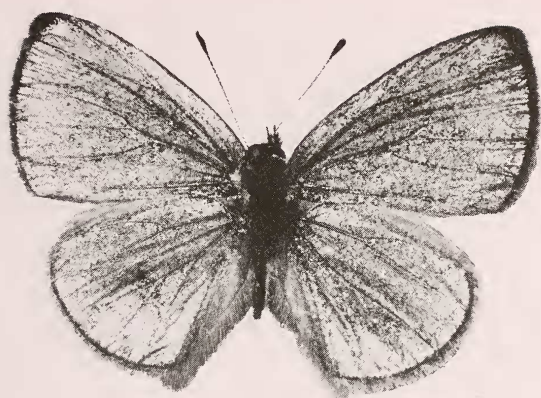


Races of *Nacaduba astarte* on island groups of the Sahul Shelf. (After Tite).

Bean: *Nacaduba* sp.

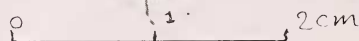
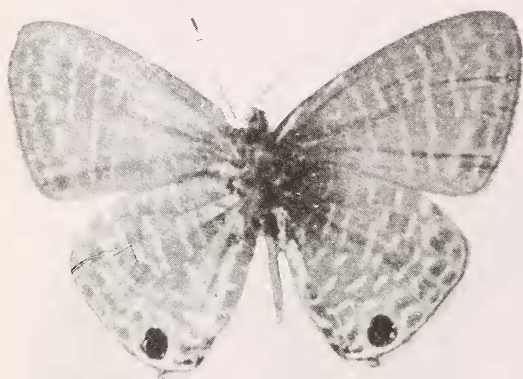
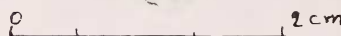
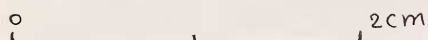
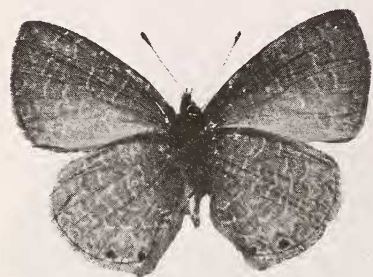


Androconia: 4. *Petrelaea dana*. 4a. *P. dana* (lower magnification). 5. *Azanus ubaldus*.
 13. *Nacaduba pactolus*. 14. *N. hermus*. 19. *N. beryae*. 20. *Prosotas aluta*.



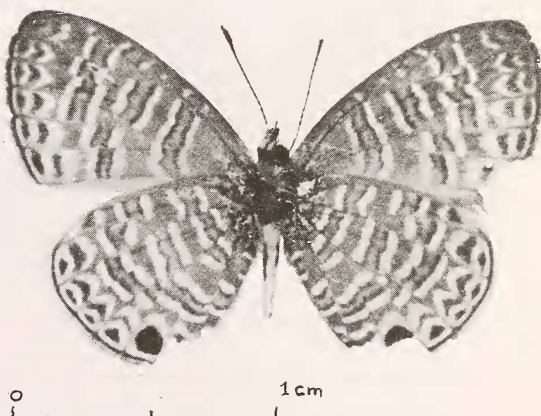
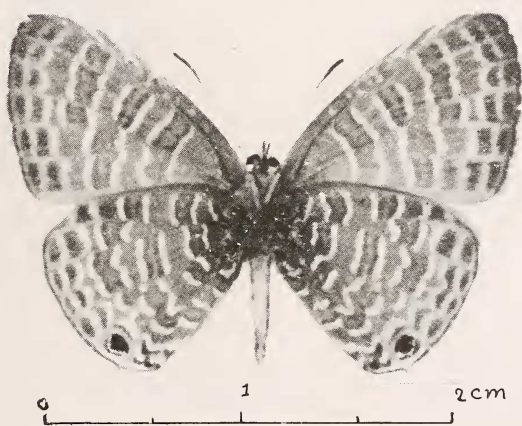
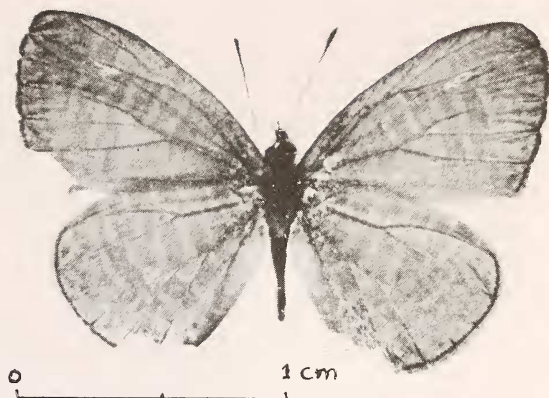
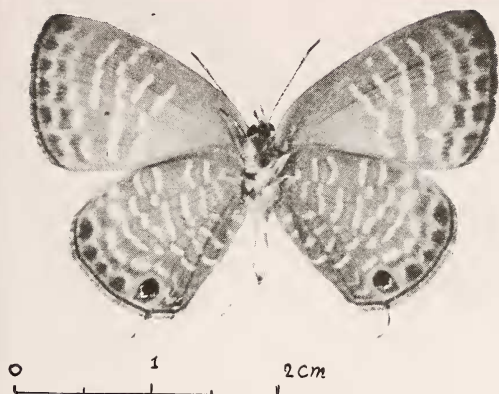
LEFT—*Petrelaea dana*: Above: male upperside, Western Ghats, October, 1961. Below: Female upperside, Manipur, September, 1957. (Photos: J. Woolmer)

RIGHT—Above: Eggshell: *Nacaduba pactolus*. Western Ghats, November, 1971. Below: *Prosotus nora*. Mahabaleshwar, November, 1971.* (Photos: E.F. Bishop)



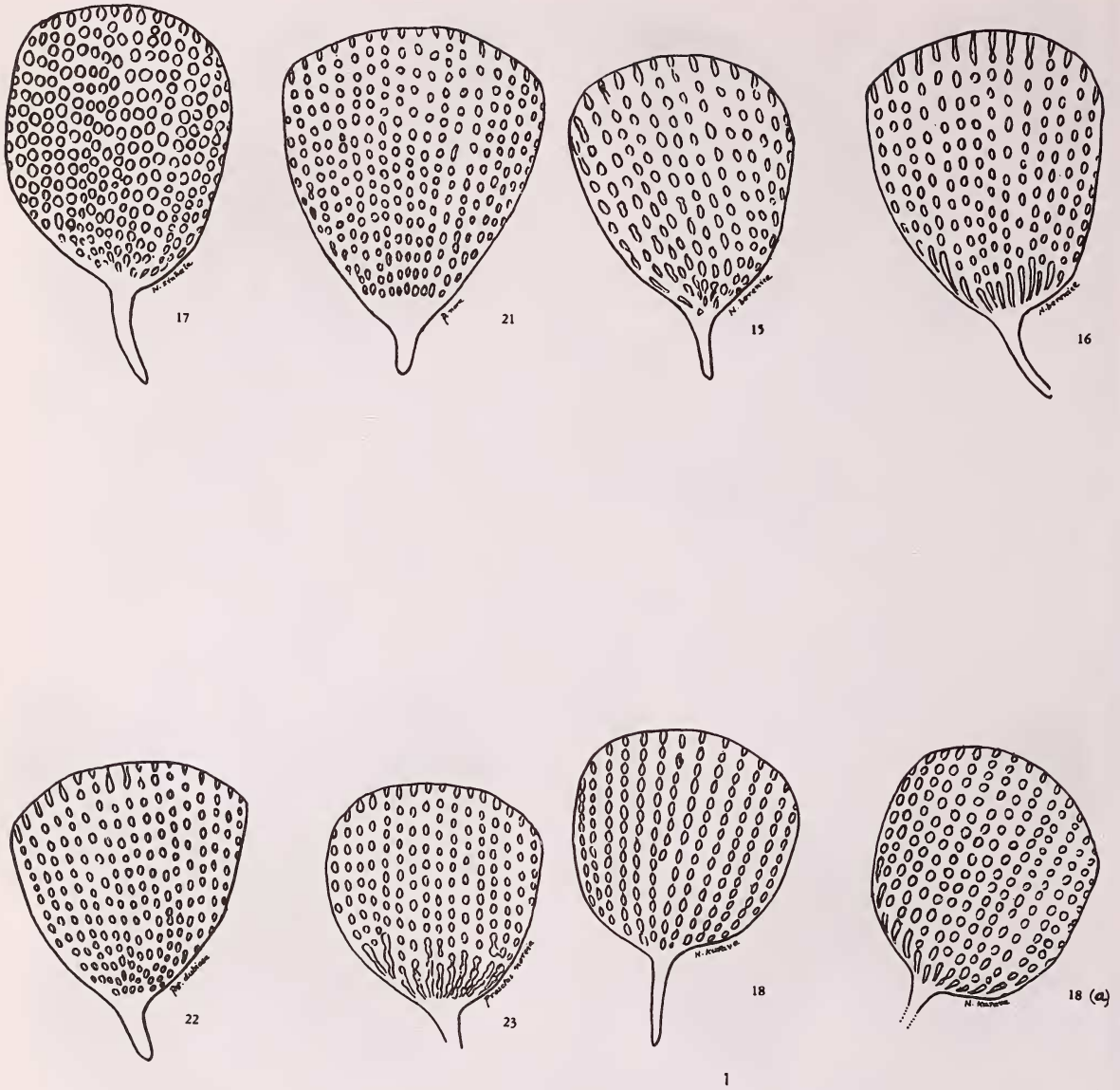
LEFT—Above: *Petrelaea dana*. Male underside. Western Ghats, October, 1961. Below: *Nacaduba beroe*. Male underside. Khasis, September, 1961.

RIGHT—Above: *Nacaduba pactolus*. Male upperside. Western Ghats, ex L. October, 1963. Below: Female upperside. Western Ghats, ex L. October, 1963. (Photos: J. Woolmer & E.F. Bishop)

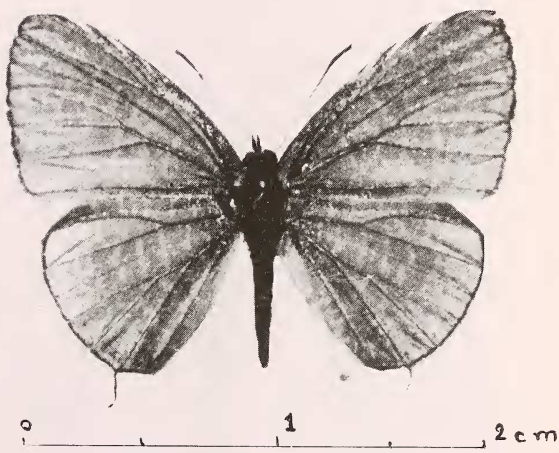
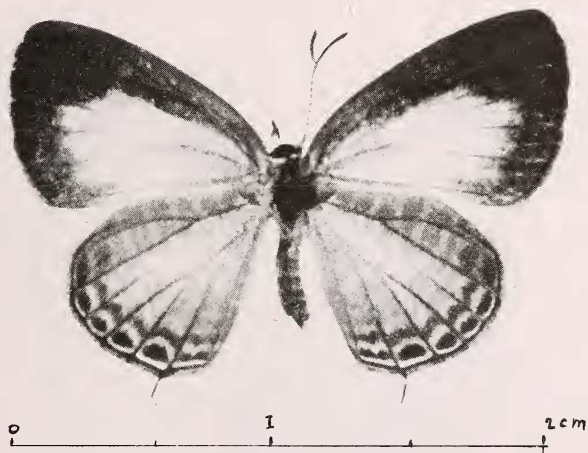
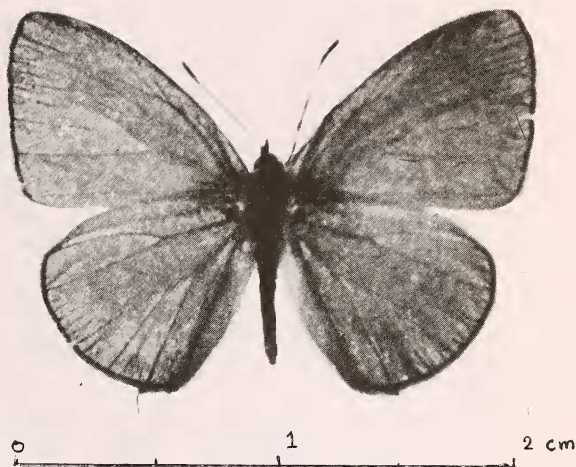
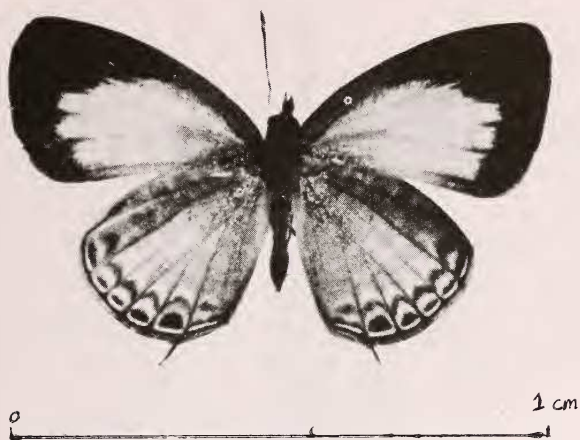


LEFT—Above: *Nacaduba pactolus*. Female underside. W. Ghats, ex L. October, 1963. Below: *Nacaduba kurava*. Male underside. W. Ghats, November, 1963.

RIGHT—Above: *Nacaduba sinhala*. Male upperside, Kandy, August, 1961. Below: Male underside. Kandy, August, 1961. (Photos: E.F. Bishop)

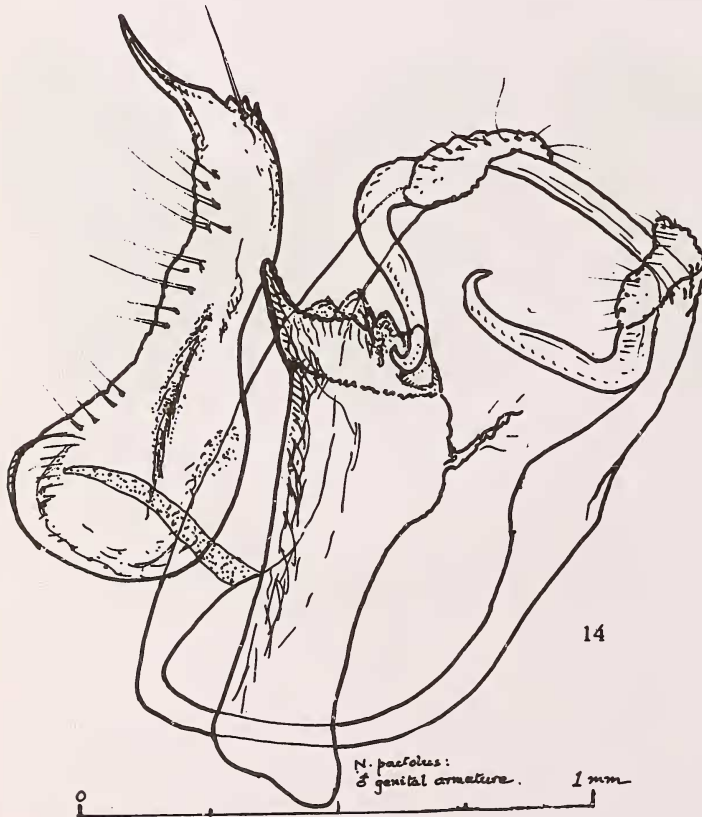
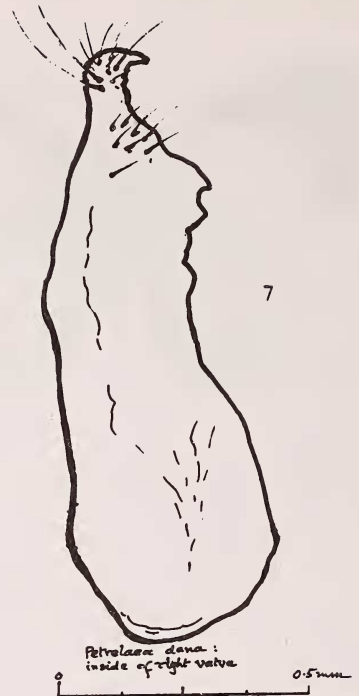
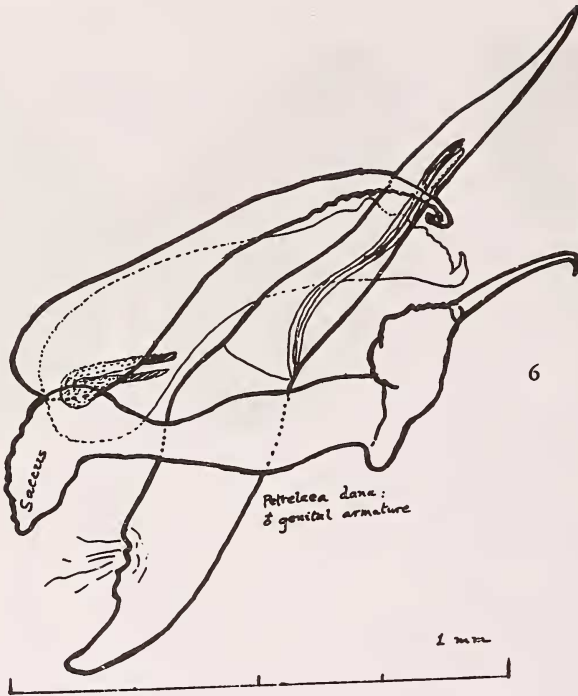


Androconia: 15 & 16. *Nacaduba berenice*; 17. *Nacaduba sinhalae*; 18 & 18a. *Nacaduba kurava*; 21. *Prosotas nora*; 22. *Prosotas dubiosa*; 23. *Prosotas noreia*.

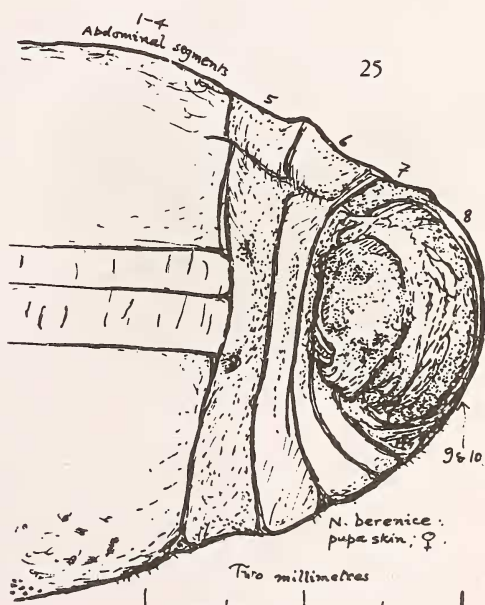
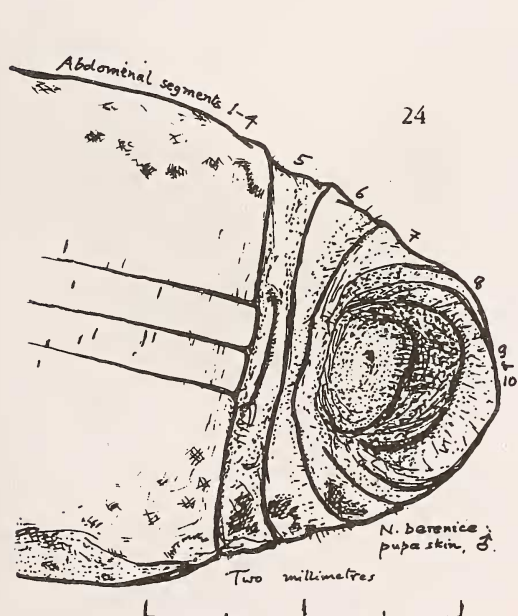
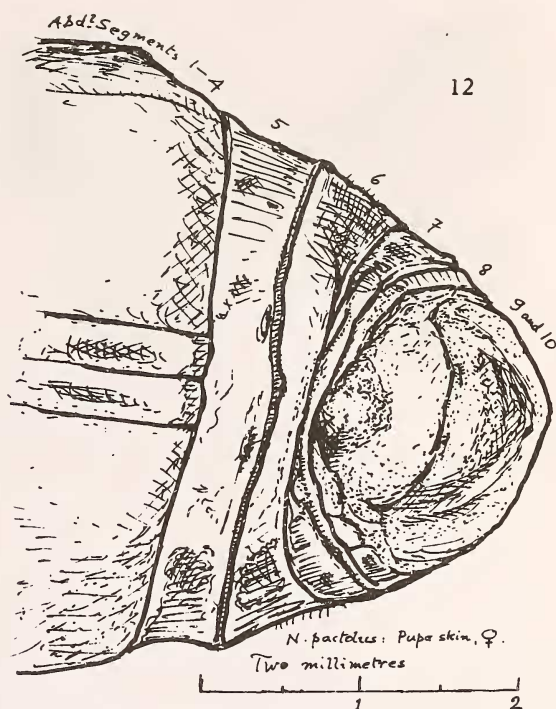
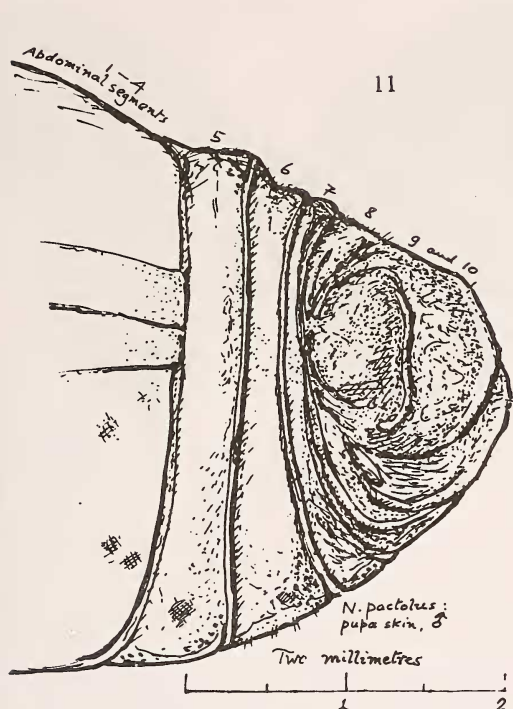


LEFT—Above: *Nacaduba sinhala*. Female upperside. Kandy, August, 1961. Below: *Nacaduba kurava*. Female upperside. Western Ghats, October, 1963.

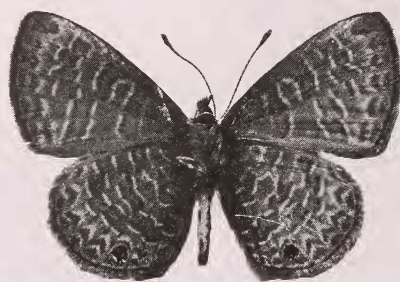
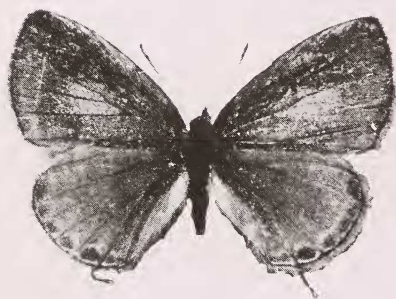
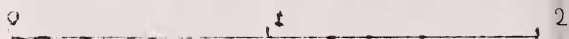
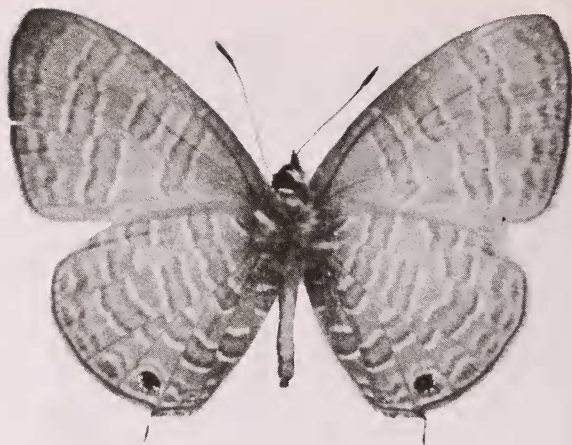
RIGHT—Above: *Nacaduba berenice*. Male upperside. Matheran, February, 1967. Below: *Nacaduba kurava*. Male upperside. Western Ghats, November, 1963. (Photos: E.F. Bishop)



Genitalia: *Petrelaea dana*—6. Complete armature; 7. Inside of right valva. *Nacaduba pactolus*—14. Complete armature; 15. Aedeagus.

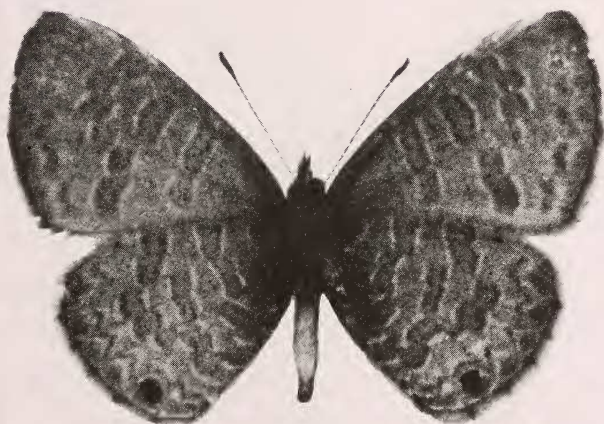
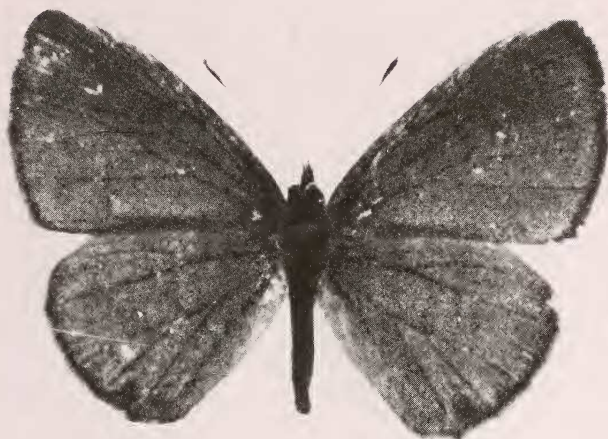


Pupa skins: *Nacaduba pactolus*. 11: Male; 12: Female. *Nacaduba berenice*. 24: Male; 25: Female.



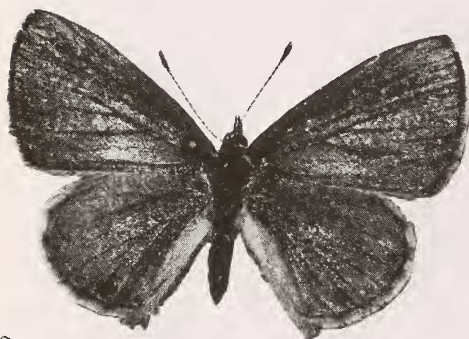
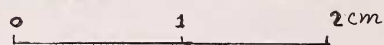
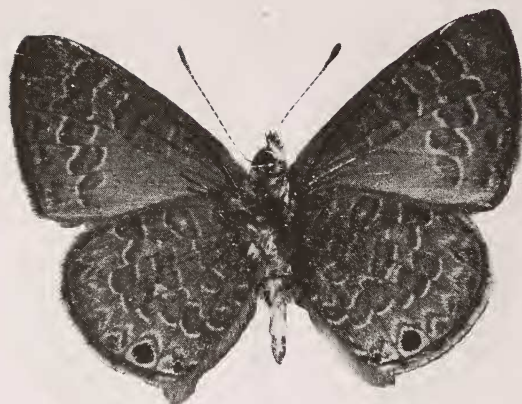
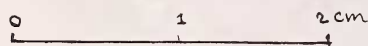
LEFT—Above: *Nacaduba berenice*. Female, upperside. Western Ghats, December, 1956. Below: *Prosotas nora*. Female, upperside. W. Ghats, November, 1971.

RIGHT—Above: *Nacaduba berenice*. Male, underside. Matheran, February, 1967. Below: *Prosotas dubiosa*. Male, underside. Western Ghats, November, 1971. (Photos: E.F. Bishop & J. Woolmer)



LEFT—Above: *Prosotas nora*. Male, upperside. Western Ghats, October, 1971. Below: Male, underside. W. Ghats, October, 1971. (Photos: E.F. Bishop)

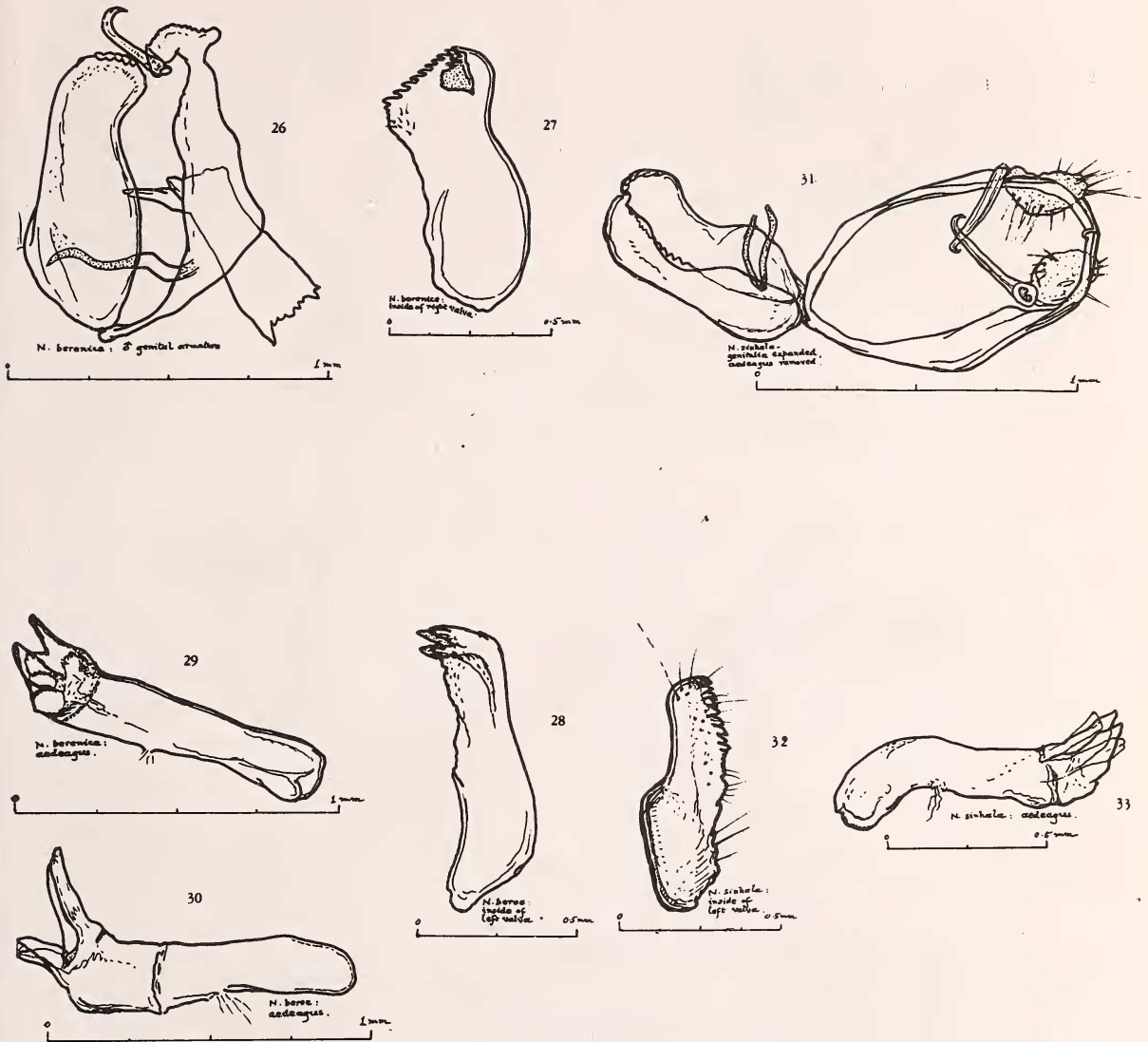
RIGHT—Above: *Prosotas dubiosa*. Male, upperside. W. Ghats, November, 1971. Below: *Prosotas noreia hampsoni*. Male, upperside. W. Ghats, September, 1964. (Photos: J. Woolmer)



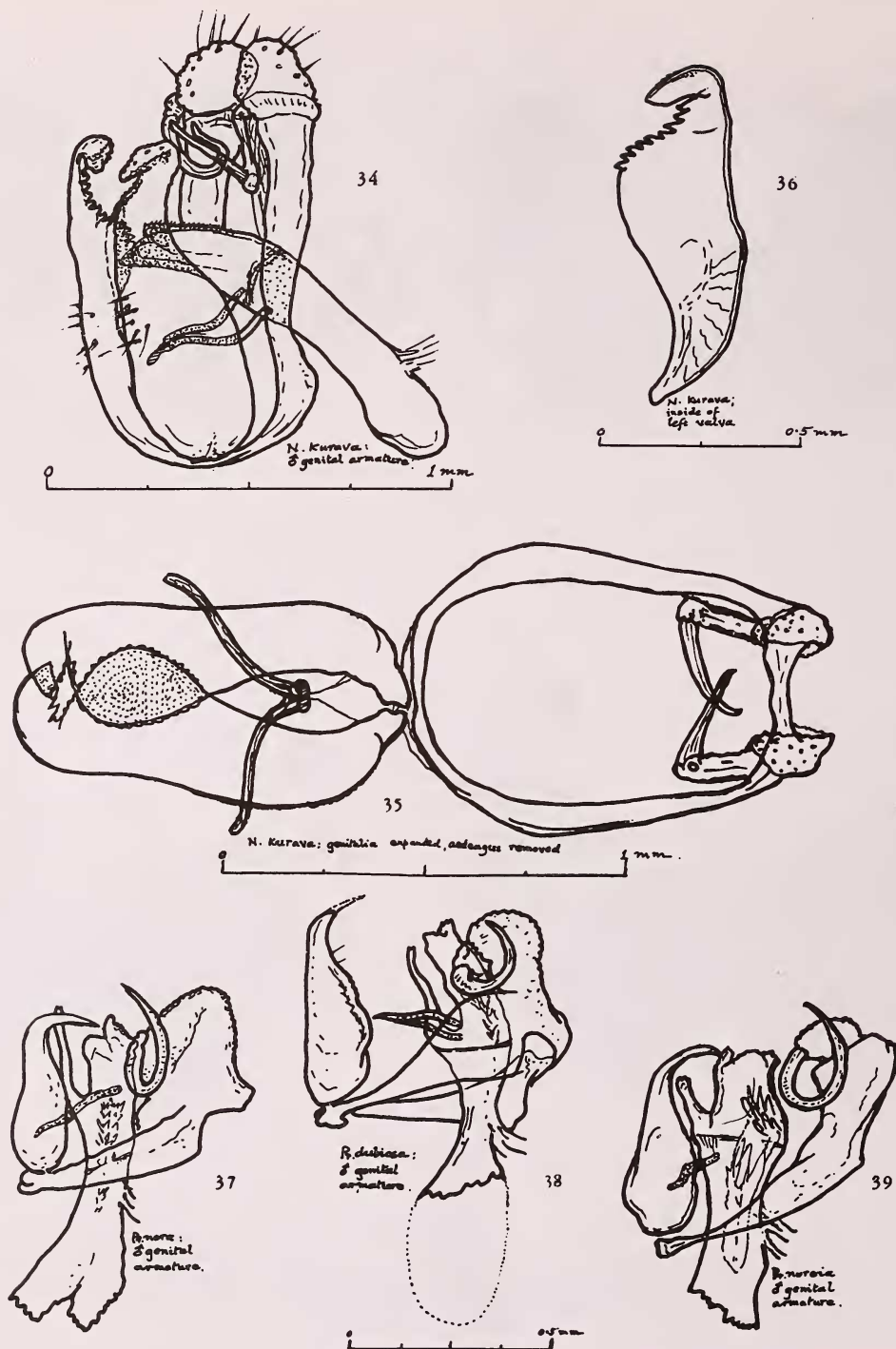
LEFT—Above: *Prosotas dubiosa*. Female, upperside. Western Ghats, November, 1961. Below: *Prosotas noreia*. Female, upperside. W. Ghats, May, 1961.

RIGHT—Above: *Prosotas noreia hampsoni*. Male, underside. W. Ghats, September, 1964. Below: *Prosotas noreia noreia*. Male, underside. Sri Lanka, August, 1961.

(Photos: J. Woolmer)

Bean: *Nacaduba* sp.

Genitalia: *Nacaduba berenice*. 26. Genital armature; 27. Inside of right valve; 29. Aedeagus. *Nacaduba beroe*: 28. Inside of left valve; 30. Aedeagus. *Nacaduba sinhalae*. 31. Genitalia expanded, aedeagus removed; 32. Inside of left valve; 33. Aedeagus.



Genitalia: *Nacaduba kurava*. 34. Genital armature; 35. Same expanded, aedeagus removed; 36. Inside of left valve; 37. *Prosotas nora*; 38. *Prosotas dubiosa*; 38. *Prosotas noreia*.

An example of the difficulties facing a species at the edge of its range was observed during the poor and untimely rains of 1971. Dr. J. F. Lobo and I found a single eggshell after a long search. The larva had just hatched, but the terminal shoot of the *Entada* seedling, on which the egg had been laid, was withered and useless as food. At first we could see no larva. Then we saw the honey-yellow little creature on the still tender yellow lateral growths or tendrils. In the end we decided to take the larva for study; I am glad to say that it was not the last of its kind, for Dr Lobo observed adults in 1973, and my colleague Fr. Wain brought me three specimens taken in November, 1974. 1971 saw a disastrous monsoon. There was virtually no rain from July until some heavy showers, from 21-23 October, which merely freshened things. We found the larva on 12 November; nearby was a fifteen-foot *Entada* loose at the roots through erosion. There ought to have been dozens of *Entada* seedlings but we only found this one. So it is clear that the species can adapt to changing conditions, up to a point. Probably in those dry conditions it lays high in the forest canopy where one can usually see some young red leaves on the thick lianas.

One hopes that this Khandalla colony is still there, and that man has not utterly ruined the habitat.

The Egg.

The egg mentioned above, or rather the shell, tallies with an example in coll. from which an adult had been reared in 1963; I measured the diameter as 0.63 mm, and the height 0.20 mm. It is a very flat egg, not at all rounded when viewed laterally, and markedly different from that of *N. berenice*, a species present in the same jungle and also feeding on *Entada*. The egg-shell is shown on Plate V, and a comparison with *berenice* in fig. 2.

Ant Relationship.

The presence of ants with the larvae is intermittent, perhaps unusual; I must have looked at dozens of larvae of all ages in the field, and only once found ants attending them. Certainly ants seemed unimportant for the development and health of captive larvae. The one rule was to rear them on the tender leaves of a growing plant. However, it is quite possible that the larvae can call up ants if they want them, for two or three *Cremastogaster* ants somehow got into one of the cages from our garden or verandah in Pune. Unfortunately the note I made at the time was badly expressed, so that it may mean I put the ants there myself. All I can now say is that I do not think I did. The ants attended the nearly full grown larva in the cage and remained with it when put into another cage.

Two *Tanaemyrmex* (= *Camponotus*) ants were taken with larvae in the field. One was a light brown form which paid some attention to a larva in captivity; I did not see the larva respond with either its double or its single ant glands. The other ant was black. In the jungle it had been attending a larva possessively but was restless in confinement. When alive, this ant held the abdomen tucked below the thorax. Fig. 4 represents this ant, probably a ♀ min. of *Tanaemyrmex compressus* (Fab., 1787).

Notes on the Anatomy of the Egg-larva.

Figure 3 is from an egg-larva taken near Khandalla in September 1964. It was preserved in Pampel's fluid, stored after a few years in ordinary surgical spirit, then mounted direct in canada balsam. The 1971 larva mentioned above was not well preserved internally, as I forgot to use Pampel's. (Surgical spirit is, I suppose, better than nothing, but it makes material brittle. It should not be used for storage; it can reduce delicate genitalia to a slimy mess).

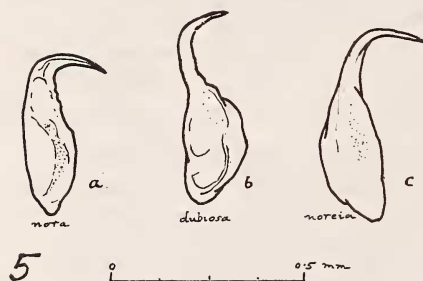
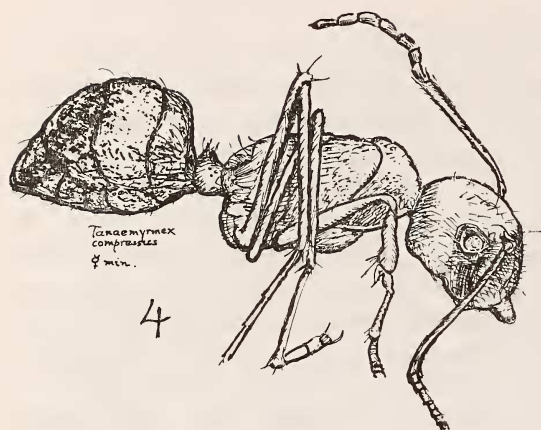


Fig. 4. Ant relationship: *Tanaemyrmex compressus* ♀ min. Fig. 5. *Prosotas* valvae: (a) *Pr. nora*; (b) *Pr. dubiosa*; (c) *Pr. noreia*.

Description of Mounted Egg-larva, Khandalla — IX-1964, S/N 2156:

The dorsal hairs are paired, as indeed in all young *Lycaenid* larvae; this is not shown in the diagrammatic figure given in Bean (1965): 615, fig. 1. It can be seen from the slide that these hairs are blunt tipped except for the pair immediately before the head. In most cases the hairs are slightly expanded towards the tip, and serrated on the forward side. There are lateral and ventrally directed hairs also, but for some reason they cannot be seen in the slide; they are clearly seen in the 1971 larva in spirit.

The chitinous rings which support the larval body are seen between the segments. The aorta can be made out as a vague line from

behind the head to the end of the body; after the thoracic segments it is thicker and functions as the heart. The digestive tract, occupying the central cavity of the body, is clearly seen below the aorta. The ganglia of the nervous system are the darker bodies in the head and above the legs and claspers.

The Pupa

Plate XI: 11 & 12 show ventral views of the male and female pupae, drawn from skins, so that I am sure of their differentiation. The distinctions may be easier to discern in the living pupa, though then, of course it is not often possible to examine the creature properly. Talbot (1938): 8, gives as an important difference the production of the middle portion of segment 10 of the abdomen in female butterfly pupae. It reaches across segment 9 as far as the middle of segment 8. My drawing shows this more as a tendency to overlapping, especially when compared with that of the male pupa. Both drawings are as true to the originals as I can make them.

NOTES

- 1) For some information on the biology of the early stages see Bean (1965): 614-626.
- 2) Wherever '*Nacaduba beroe*' is mentioned in the 1965 Article read '*Nacaduba berenice*'. See also below, p. 39, note.
- 3) *Entada* seedlings may be easily transported during the rains, after they have sprouted and are still attached to the seed. Dry seeds may be encouraged to germinate by filing at the scar until the grey endosperm can be seen.

The Male Genitalia

Plate X: 14 was drawn from a partially successful attempt to expand the genitalia flat. I ought first to have removed the aedeagus. However, the result showed most of what is required, so I drew the figure as follows: The left valve, rather displaced, shows its inside with part of the furca near its base. The right valve is omitted for the sake of clarity. The

aedeagus remains roughly in its true position between valves and labides. The latter, with their falces, are also in their position, on the genital ring.

The *valvae* are shaped like the bill of a cormorant, and are characteristic of this species. This is useful under field conditions, when the genitalia of a worn four-line *Nacaduba* can be squeezed forward and seen with a hand lens to verify identity.

The terminal spike is directed ventrally. The inside of the valve is folded into a ridge from near the base to about half way up. This ridge is covered with tiny hooks or cornuti. Towards the tip of the valve ventrally there are rather shallow serrations, and three prominent teeth dorsally, near which a major bristle arises.

Aedeagus. The ductus enters dorsally, as in the whole *Nacaduba* section, and is clearly seen in the slide as a tube of light consistency, not of chitin. (Plate X: 14). The ductus usually only appears vaguely after preparation, as in Plate X: 15. The aedeagus in Plate X: 14 seems to be lying on its left side, more or less; the most prominent terminal process is the single lobed Chapman's process, and the other projections belong to the partially everted penis. Below the Chapman's process is the zone, a girdling ridge which helps steady the aedeagus. Plate X: 15 is a dorsal view of the organ. Proceeding from above the zonal ridge are two rounded, ventrally hollowed lobes which correspond in position to the two-horned appendage in *Petrelaea*. (See fig. 1). The slightly swollen, cloven base of the aedeagus I take to be the coecum; (Latin = 'blind'; here the closed or blind end of the organ).

The *Labides* or divided uncus characteristic of the *Lycaenidae* seem to be of normal pattern in this species. The falces are somewhat flattened dorso-ventrally.

Note on the Androconia of the Nacaduba Complex.

As stated above under *Petrelaea* (p. 17) these can only be properly studied with the aid of the scanning electron microscope. I can, therefore, only give highly provisional information, and that about only eleven species.

The scales are scattered among the ordinary cloaking scales on the upper sides of the forewings. Each is attached to the wing by a footstalk or pedicel. The scales studied, except *Petrelaea*, are shaped like a Burmese fan or a table-tennis bat. In Table 4 'fan' means the scale is longer than wide, and 'bat' that it is roughly as broad as long. Some scales are symmetrical (S) or asymmetrical (A). The pedicels merge gradually into the body of the scale except in *pactolus* where the scale springs at right angles from the pedicel in a slightly excavate line.

III. *Nacaduba berenice plumbeomicans*

(Wood-Mason & de Niceville, 1880)

(Plates IX & XII)

This species extends from Sri Lanka through peninsular India eastward to the Solomons, Queensland and Northern Australia. The Indian race extends from the Western Ghats to Burma and the Andamans.

Identification.

Until recently I thought my Western Ghats material was of *N. beroe gythion* Fruh. Evans (1932): 243, and Evans & Cantlie (1962): 79 make it the only species from the Western Ghats with hairs or hair-like scales on the discs, so I jumped to the conclusion I had *beroe*. It was only when I came to look at the genitalia that I found the valves quite different from those of *beroe* figured by Tite (1963) 89, fig. 16. I had an opportunity of showing my slide to Mr. Tite who considered it to be of *berenice*. The Hope Collections material of

TABLE 4

SOME ANDROCONIA OF THE *Nacaduba* COMPLEX

Text-figure		Shape	Symmetrical or Assymetrical	No. of 'Ridges'
4/4a	<i>Petrelaea dana</i>	Rod-like, swollen at ends, distal end larger.	—	8-10; i.e. (4-5 each side)
13	<i>Nacaduba pactolus</i>	Bat; sides nearly parallel.	S	16
14	<i>N. hermus</i>	Bat; rounded sides.	A	15
15/16	<i>N. berenice</i>	Fan; converging sides.	A or S	14-15
17	<i>N. sinhala</i>	Fan, parallel sides	A	18
18/18a	<i>N. kurava</i>	Fan, rounded sides	S	14
19	<i>N. beroe</i>	Fan; rounded sides	A	14
20	<i>Prosotas aluta</i>	Fan; elongate like auk's egg	S	15
21	<i>P. nora</i>	Fan; curved, converging sides.	S	19
22	<i>P. dubiosa</i>	Fan, as in <i>nora</i> , smaller, converging sides angled in middle.	A	17
23	<i>P. noreia</i>	Bat; rounded sides	A	16

N. berenice plumbeomicans comes from Assam, the Eastern and Western Ghats right down to Cape Comorin, but there are no *N. beroe* specimens from peninsular India. *N. beroe* would seem to have its headquarters from Sikkim into Assam and Burma, meeting *N. berenice* only in the last two areas and in Sri Lanka.

After several examinations of genitalia I felt confident in assigning my Western Ghats material of this species to *N. berenice*. The experience has taught me not to make mere distribution a deciding factor. If I had referred to Bell's beautifully accurate description of '*Nacaduba plumbeomicans*', Bell (1918) 661-662, I might well have arrived at the correct identity without genitalia examination.

Table 5 shows that the two species can almost always be distinguished by facies in the

male, even with worn examples; and that genitalia are an absolute check. See Plate VI for a male underside.

EARLY STAGES

Egg-laying.

On 4.xii.1957, between 13 and 14 hrs, I found females laying in a hot glade of climax jungle near Khandalla, Western Ghats, at about 650 metres altitude. The place was probably a woodcutters' clearing. The undergrowth formed a thick barrier at the end; and there the sun caught it during the hottest part of the day. The butterflies were being attracted to a point where some long trailers from *Entada* seedlings sprawled over the tangled growths of other plants.

It seems likely that on this site a great number of eggs were being laid on a few

OCCURRENCE AND HABITS OF THE NACADUBA

TABLE 5
DETERMINATION OF TWO *Nacaduba* SPECIES

<i>N. berenice</i>	<i>N. beroe</i>
Above:	Above:
1) Violet blue, frosted appearance.	1) Dark violet blue.
2) May be slightly transparent on hind wing.	2) Always quite opaque.
3) Discs of wings bearing hairlike scales, but sparsely even in fresh specimens.	3) Discs covered with white hairlike scales, abundant even in a rubbed specimen.
4) Apex of forewing rounded.	4) Apex of forewing produced.
5) Termen of forewing convex.	5) Termen of forewing straight in middle.
Below:	Below:
Catenulated bands shaded between the strigae, as in <i>Prosotas nora</i> , though the ground colour is not darkened.	Catenulated bands not shaded between the strigae, as in <i>N. kurava</i> .
<i>Genitalia</i>	<i>Genitalia</i>
Valva-broad; almost square serrated end, the ventral side of which is curled.	Valva-narrow; not serrated at end, but there are beaklike processes at the tip.
Aedeagus — The double Chapman's process is shorter.	Aedeagus — The double Chapman's process is longer.

plants in a small area. I have never seen the butterflies laying except on young tender red leaves. The great lianas of *Entada* do not produce many of these, especially in December, when the ground is drying up, and for the same reason there are fewer tender leaves on the seedlings which have survived after the rains. Consequently the *berenice* larvae may be reduced in numbers through starvation and cannibalism. They are well protected by colour and habits, but predators must find them more easily when they are crowded. And they must often be crowded, since both female and larvae require tender leaves only, and such leaves often occur where the sun does not warm them sufficiently to encourage egg-laying.

On two sprays of *Entada* bearing young red leaves there were about sixteen eggshells, seven to ten young larvae about 1.5 mm long, and one larva of 2.5 mm. They were on leaves and stalks, all looking very like the bracts of

the plant. The observer's confusion is increased because the axils of the compound leaves of *Entada* have a dark base, so that the axil looks like some kind of larva with a dark head. Near one of these axils was an empty eggshell and just beside it a newly emerged larva; soon it would begin the long upward climb to its first leaf meal. Judging by many eggshells seen in the field it seems that the emerging larva only eats a little of the shell — enough to get out, or a little more.

Egg.

According to a Ms note of 1957 the ground colour of a newly laid egg is yellow, but the general effect is whitish, because of the colour of the surface sculpture. Bell (1918): 662, must be credited with first pointing this out. It was noticeable when comparing this egg with that of *N. pactolus* which I found in the same locality, and often at the same time. The